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Summary

Drifting larvae of one anadromous (*Leucopsarion petersi*) and three amphidromous (*Chaenogobius annularis*, *Tridentiger brevispinis*, and *Rhinogobius* sp. CB) gobioids (Gobiidae, Teleostei) were collected over 24 h into server nets in the tidal and non-tidal zones of the Natori River (northern Japan) to study the downstream migration of these species in the lower course of the river. The larval body sizes of all three amphidromous species declined from the beginning to the end of the 3-month spawning season, apparently due to decreases in the egg sizes.

Drifting larvae, mostly at the yolk-sac stage, were caught mainly between dusk and dawn. Diel changes in the number of larvae collected showed one to three steep peaks of abundance. Analysis of the timing of the peaks in relation to the spatial distribution of the spawning grounds of each species indicated that there were two sources of larval gobioids caught in the tidal zone, larvae that had drifted downstream on the river current from nests above the collection station and larvae that were pushed upstream by tidal currents from sites below the station after they had entered the estuary.

Introduction

Most freshwater gobioids are diadromous (1-4). They descend the river to the sea soon after hatching from eggs that are attached to a nest positioned under stones in the river (5); in the estuary they meet a drastic environmental change from freshwater to a saline environment. Estuaries seem to be areas to intermediate conditions that are important in the process of adaptation to a saline environment (4). Therefore, the spatiotemporal details of the seaward migration of larval fish should be studied in order to clarify the role of estuaries in adaptation to salinity.

Although many diadromous fish (6-9), and amphidromous gobioids (10), migrate downstream at night, the behavior of larval gobioids in the lower river course has not been described in detail. In the present study, spatiotemporal changes in the number and developmental stage of drifting larval gobioids in the lower course of a river were analyzed.

Materials and Methods

Collection Methods

Drifting larvae were collected two or three times a month from May to September 1995 at stations, one in the Natori River and one in the Hirose River (Fig. 1). The tidal zone of the Natori River extends up to 8 km from the river mouth, and the two rivers meet each other at that point. At station A (St. A), about 7 km upstream from its mouth, the river is 30 m wide, the flow is predominantly normal and/or slow, and the depth varies by about 0.6 m due to tidal effects. At station B (St. B), about 9 km from the mouth of the Natori River, the river is 25 m wide and there is a complex flow regime composed of rapids, normal and slow flow zones, and pools, all without tidal effects.

Larvae were collected using a server net of 0.5 m \times 0.5 m (mouth opening) \times 2.5 m (length) made of 0.457 mm mesh. Larvae were collected for successive 1-h periods against a downstream normal flow at each station at a place where the river was about 0.3 m deep. The water temperature, salinity and flow velocity of

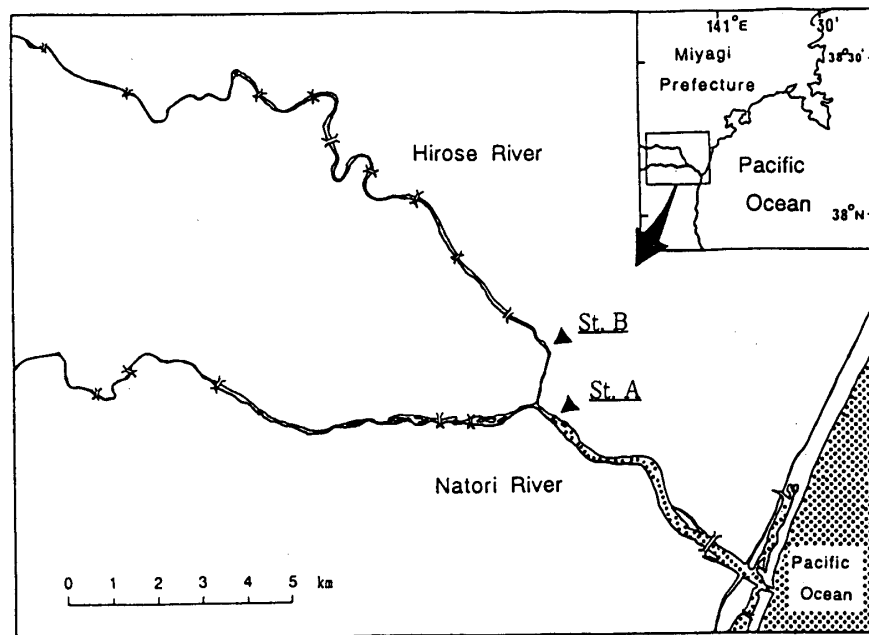


FIG. 1. Map of the study area showing the locations of the sampling sites in the Natori and Hirose rivers.

the surface layer, and the depth, were measured at the beginning of each collection period. The larvae were fixed in 10% formalin immediately after being caught and later were sorted by species in the laboratory. The developmental stage was judged from the external morphology and the total length was measured.

Nests, located under stones, and adult gobioids were counted at both stations. Eggs and adult gobioids were collected and immediately fixed in 10% formalin. Major axis of the eggs were measured and species identification was performed for the adults after returning to the laboratory.

Collection Periods and Frequency

To study the diel larval drift patterns, consecutive 1-h samplings were conducted at both stations for 24 h on each of four separate occasions. Sampling began in the daytime on May 22, May 29, July 10 and July 19, 1995.

To study seasonal changes in larval numbers and developmental stages, consecutive 1-h samplings were conducted at both stations for several hours around sunset on eight separate occasions in addition to four 24-h collections. Sampling began at a few hours before sunset on May 9, May 17, June 12, June 19, June 29, August 2, August 30 and September 14, 1995.

To determine the duration of the spawning season, adult gobioids and eggs were collected, and nests were counted, on all of the days listed above, as well as on April 26, 1995. In 1996 gobioid eggs were collected only at St. A on June 4, July 16 and August 27 to study the seasonal changes in egg sizes.

Results

River Conditions, Gobioid Species and the Duration of the Spawning Season

The water temperatures measured at Sts. A and B were similar, rising from mid-May to early August and declining thereafter (Fig. 2). The salinity was very low at St. B with a narrow range, 0.01 to 0.02. The salinity was also low at St. A but the range was wider, 0.02 to 0.16 except for a reading of 2.10 on August 2.

The larval and adult gobioids collected were of four species: one anadromous species, *Leucopsarion petersi*, and three amphidromous species, *Chaenogobius annularis*, *Tridentiger brevispinis* and *Rhinogobius* sp. CB.

Seasonal changes in the number of nests at both stations are presented in Fig. 3. *C. annularis* nests were found at St. A on April 26 and were found at St. B on June 12 and 19, although adults were found at both stations throughout the sampling period. Adult *L. petersi* were found only at St. A from late April to late May, and only two nests were found there (on May 9). Adult *T. brevispinis* were abundant at both stations at every sampling time. Their nests increased in number at St. B from June 12, peaked from June 19 to July 10, and then decreased abruptly. At St. A *T. brevispinis* nests were abundant 1 month later than at St.

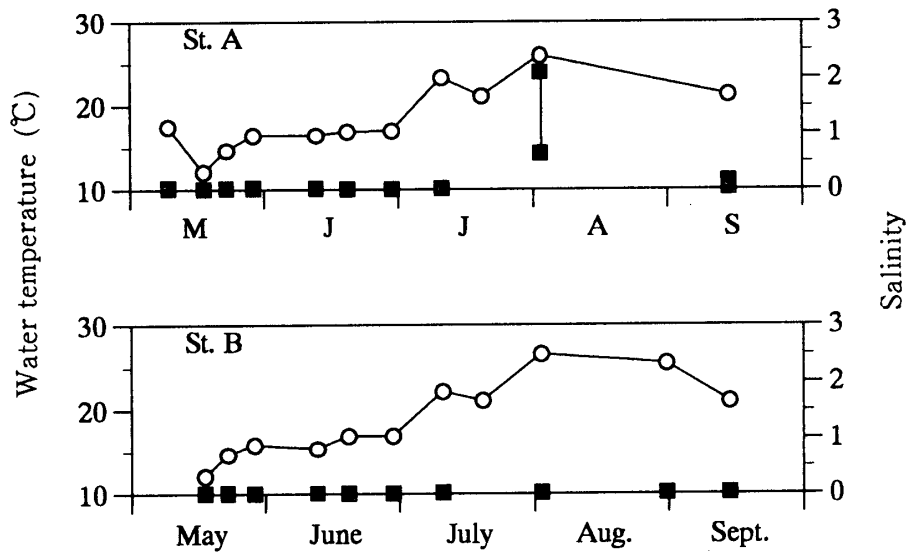


FIG. 2. Seasonal changes in the surface water temperature at sunset and salinity ranges at Sts. A and B. Negligible variation in the salinity was observed except on 2nd August at St. A.

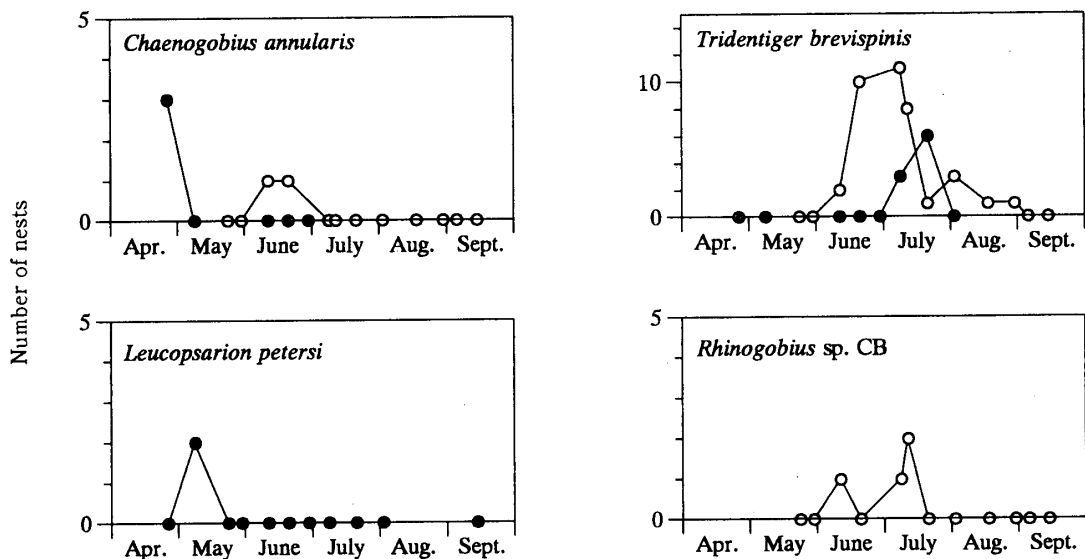


FIG. 3. Seasonal changes in the number of nests found from April to September. Solid and open circles denote Sts. A and B, respectively.

B; nests were first found on July 10, peaked on July 19 and were absent in August. Adult *Rhinogobius* sp. CB were caught only at St. B, and only a few nests were found, also at St. B, from June 12 to July 12.

Seasonal Changes in Numbers, Developmental Stage and Body Length of Drifting Larvae

Seasonal changes in the number of drifting larvae are presented in Fig. 4.

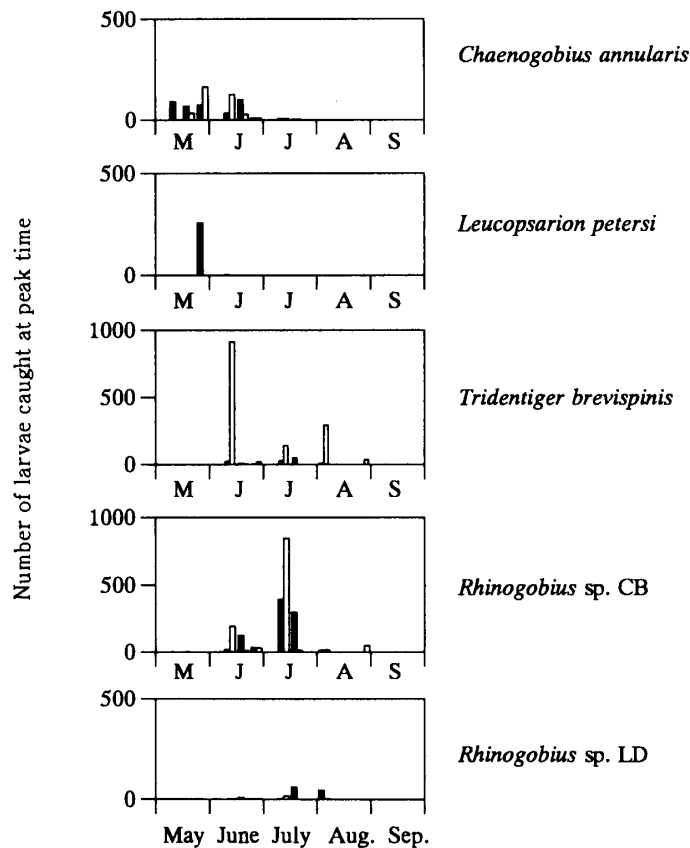


FIG. 4. Seasonal changes in the maximum number of drifting larvae caught from May to September, 1995. Solid and open squares denote Sts. A and B, respectively.

Larval *C. annularis* were present from May 9 to July 19, whereas *L. petersi* larvae were present from May 29 to June 12, and *T. brevispinis* and *Rhinogobius* sp. CB larvae were present from June 12 to August 30. A few larval *Rhinogobius* sp. LD were also observed.

The drifting larvae of each species that we collected were all at the yolk-sac stage except for five *Rhinogobius* sp. CB larvae, caught at St. A on August 2, which were at the preflexion stage. A significant decrease in larval body length over time was observed for *C. annularis*, *T. brevispinis* and *Rhinogobius* sp. CB (ANOVA; *C. annularis*, $F=26.74$, $p<0.001$; *T. brevispinis*, $F=78.80$, $p<0.001$; *Rhinogobius* sp. CB, $F=32.92$, $p<0.001$; Fig. 5). *T. brevispinis* showed the most rapid decrease in size, 15.7% over 3 months. The major axis of the pre-eyed and eyed eggs of *T. brevispinis*, collected at St. B in 1995 and at St. A in 1996, also became smaller during the 3-month spawning season (ANOVA; eyed egg, $F=77.71$, $p<0.001$; pre-eyed egg, $F=65.63$, $p<0.001$; Fig. 6).

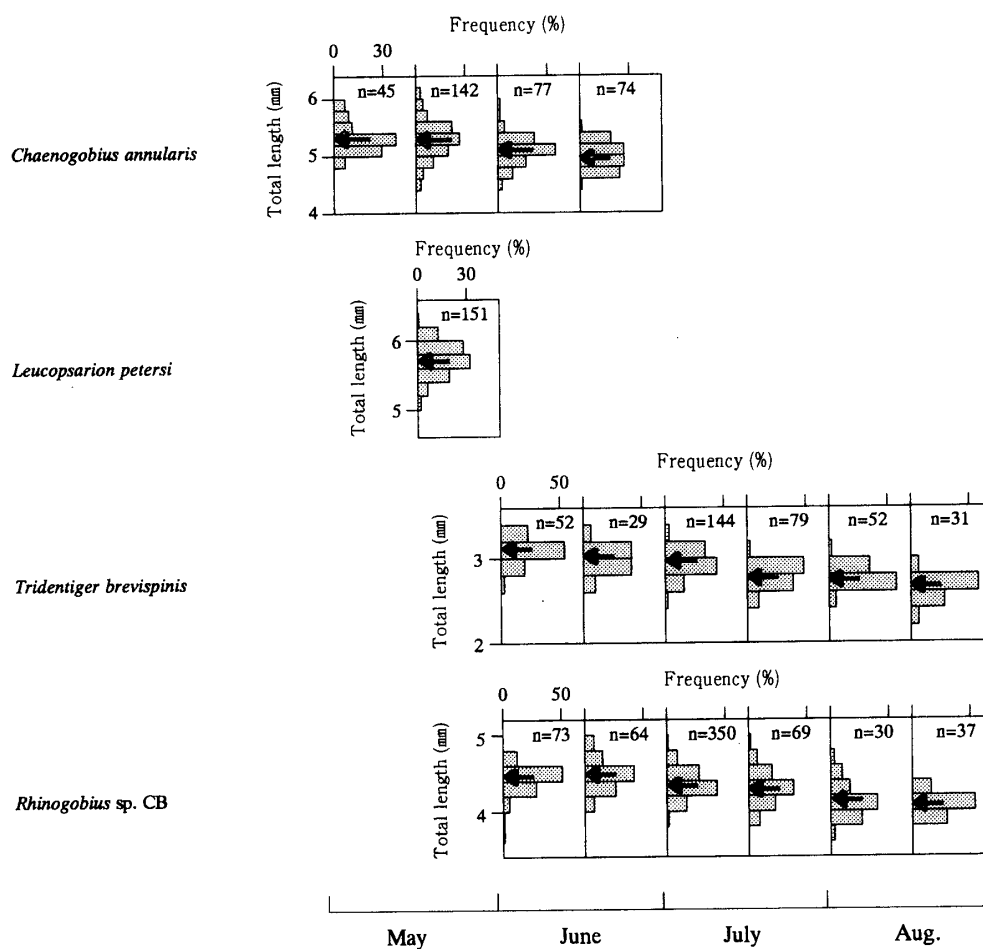


FIG. 5. Seasonal changes in the total length distribution of drifting yolk-sac larvae from May to August, 1995. Arrows denote mean larval sizes. Significant differences were detected for *C. annularis*, *T. brevispinis*, and *Rhinogobius* sp. CB ($p < 0.001$ in each case).

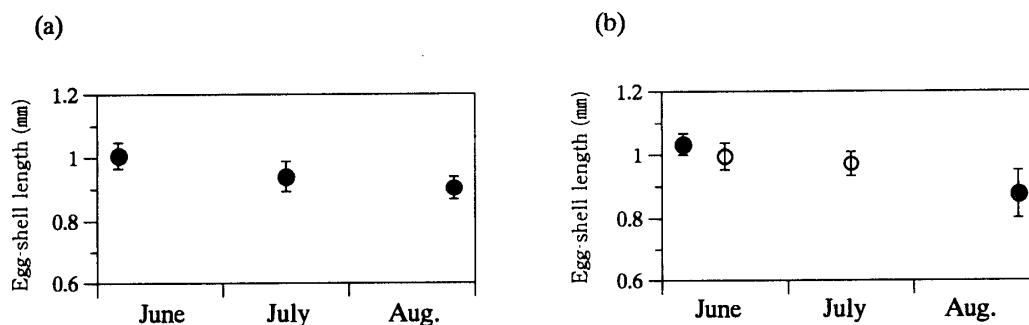


FIG. 6. Seasonal changes in the egg-shell length of *Tridentiger brevispinis* from June to August. The data are the means \pm SD. (a) Pre-eyed eggs, (b) Eyed eggs. ●: Spawned at St. A in 1996, ○: Spawned at St. B in 1995.

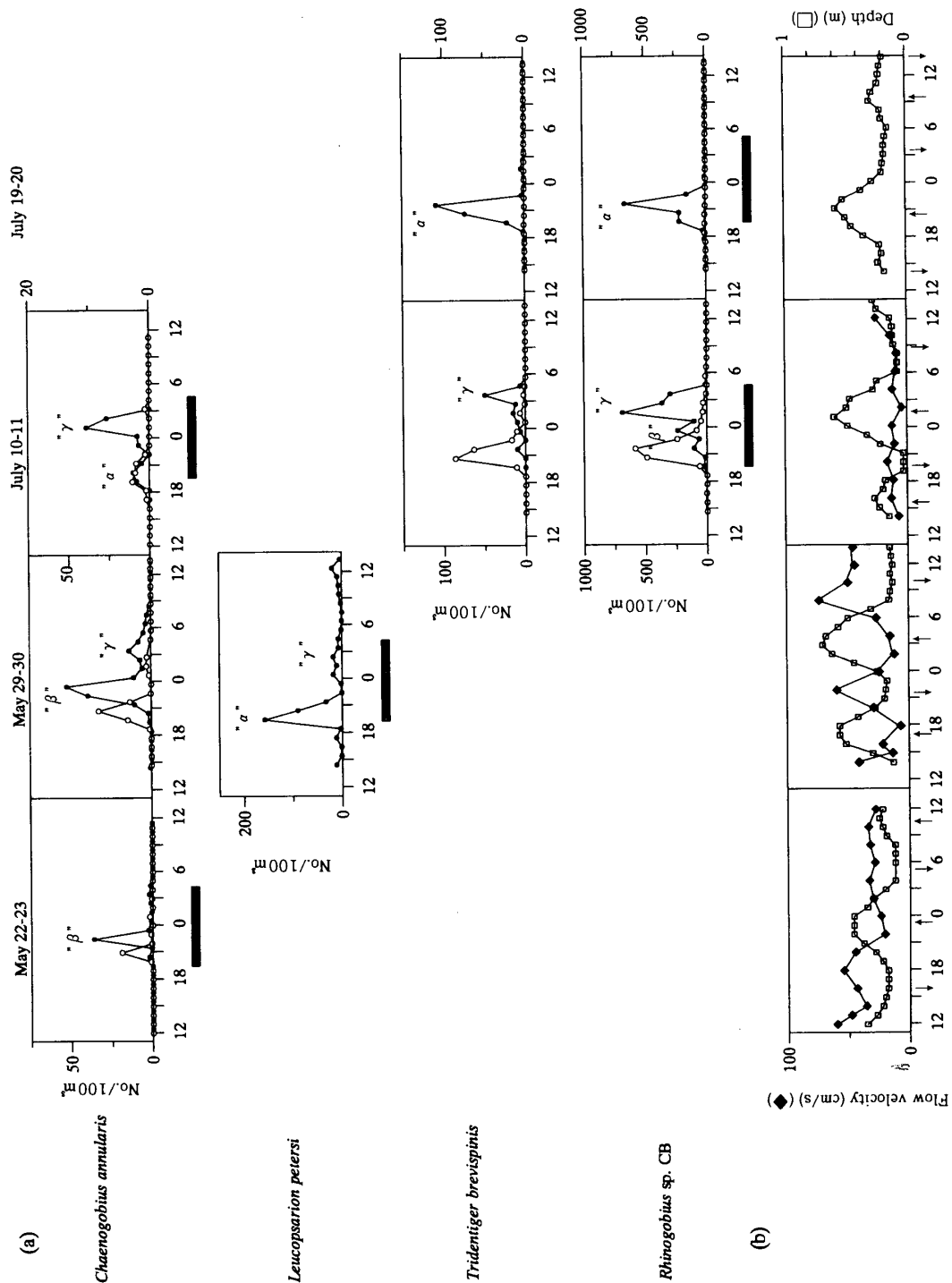


FIG. 7. (a) Diel changes in the number of drifting larvae. Solid and open circles denote Sts. A and B, respectively. The black bars under the abscissa show the night. (b) Changes in the surface downstream flow velocity and in the depth at the net position at St. A. Up and down arrows below the abscissa show the times of flood and ebb, respectively. The symbols of α , β and γ indicate the peak types at St. A.

Diel Changes in the Number of Drifting Larvae

Diel changes in the number of drifting larvae caught during four 24-h sampling periods are shown in Fig. 7. Drifting larvae were caught at both stations mainly between dusk and dawn. There was one steep peak of abundance at St. B, 2 to 3 hours after sunset, and three peaks of abundance were seen at St. A, which we refer to as the α , β and γ peaks: the α peak occurred immediately after sunset or almost at the same time as the single peak at St. B, and the β and γ peaks occurred 1–2 and 6–7 h after the single peak at St. B respectively. The α peak seemed to have no relation to the tidal cycle given that the *C. annularis* α peak occurred at the ebb on July 10–11, whereas the α peak of *L. petersi* on May 29–30 and those of *T. brevispinis* and *Rhinogobius* sp. CB on July 19–20 occurred during the flood. The β peak also seemed to be unrelated to the tidal cycle, as shown by the discordance between *C. annularis* abundance and the tidal stage seen on May 22–23 and May 29–30. By contrast, all of the γ peaks of abundance occurred during the flood stage of the tidal cycle.

Discussion

The larvae of the anadromous fish *L. petersi* were present in the Natori River for only 2 weeks, which is a very short period compared to the presence of the amphidromous gobioids *C. annularis*, *T. brevispinis* and *Rhinogobius* sp. CB. The reasons for this difference is probably the short spawning period of *L. petersi* (3).

A gradual decrease in the body size of the drifting larvae was seen as the season progressed for *C. annularis*, *T. brevispinis*, and *Rhinogobius* sp. CB (Fig. 5). This change probably reflected reduced larval size at the time of hatching rather than a difference in larval growth after hatching because the sizes of the drifting larvae did not correlate with the volume of remaining yolk. On the other hand, pre-eyed and eyed eggs of *T. brevispinis* collected in late August were at least 10% smaller across the major axis than those collected in early June 1996 (*t* test; $p < 0.001$). Therefore, the decrease in body size of the drifting larvae might have been related to the decrease in egg size, and not to a change of larval growth during their drifting life. Although variation in egg size has been reported for many marine and freshwater fish, e.g. amphidromous *Plecoglossus altivelis* (11) and *Tridentiger obscurus* (12), it is difficult to identify a causal factor because it varies among species and among habitats (13).

Larval drift was observed mainly at night for all four species throughout the sampling period, and each species showed at least one peak of abundance after sunset at one or both stations. Iguchi and Mizuno (14) reported that newly hatched larval *Rhinogobius brunneus* show a changed phototactic response, from negative to positive, and move upward in response to the feeble light at sunset. They suggested that this change in phototaxis triggers the passive transportation

of larval gobionids by river currents, beginning at sunset. This explanation may also be true for the larval drift observed in the present study.

Most of the drifting larvae of *C. annularis*, *T. brevispinis* and *Rhinogobius* sp. CB were caught in the first few hours after sunset at St. B. These species were probably present further upstream as well as at spawning sites at St. B. Considering that this station showed a negligible tidal effect, it is likely that the drifting larvae captured at this station were transported from upstream spawning grounds by downstream currents, rather than being carried upstream from lower sites by tidal currents.

Three peaks of abundance of drifting larvae were seen at St. A. The α peak of *L. petersi* was observed on May 29–30, those of *T. brevispinis* and *Rhinogobius* sp. CB on July 19–20, respectively (Fig. 7). This peak occurred a few hours after sunset so the larvae must have been transported from an area close to St. A because they begin drifting away from their nests at sunset. The α -peak larvae of *L. petersi* and *T. brevispinis* probably originated from upstream spawning grounds near St. A, because adults and nests of *L. petersi* and *T. brevispinis* were seen at St. A around the day of larval sampling. Although nests of *Rhinogobius* sp. CB were found at St. B but not at St. A, it is probable that nests of this species were also located upstream from or close to St. A.

C. annularis β peaks were seen on May 22–23 and May 29–30, and a small *Rhinogobius* sp. CB β peak was seen on July 10–11 (Fig. 7). The β peak occurred about 1.5 h after the single peak at St. B in the case of *C. annularis* on May 22–23. The time lag of 1.5 h agrees with the time of 1.6 h estimated for larvae to drift from St. B to St. A under the flow conditions of that day (mean, 35 cm/s). In other cases the β peak could be explained similarly. This finding suggests that the β -peak larvae seen at St. A also composed the single peak seen at St. B.

On May 29–30 γ peaks of *C. annularis* and *L. petersi* were seen and on July 10–11 γ peaks of *C. annularis*, *T. brevispinis* and *Rhinogobius* sp. CB were seen (Fig. 7), although the peak of *L. petersi* was small. The γ -peak larvae may have been pushed upstream by the rising tide after having reached the area of the river lower than St. A, because the peak occurred at about high tide on each occasion, and because the time lag between the single peak at St. B and the γ peak at St. A was too long to be due to the direct movement of larvae from St. B to A on a downstream current. Although an upstream current was not detected at St. A there may have been an upstream current in the deep water in the center of the river, which would not have been detected because the sampling site was in shallow water close to the bank. Furthermore, the γ -peak larvae tended to be larger than those of the other peaks for every species (Table 1) and this difference in size was significant for *T. brevispinis* and *Rhinogobius* sp. CB on July 10–11 (ANOVA; *T. brevispinis*, $p < 0.001$; *Rhinogobius* sp. CB, $p < 0.01$). This finding suggests that the γ -peak larvae had drifted for longer than the larvae of the other

TABLE 1. Comparison of the mean total length in millimeters of drifting larvae between the abundance peaks and among the species (mean \pm SD).
Numbers in parentheses indicate sample sizes.

Date	Species	St. B	α , β (St. A)	γ (St. A)	F value
29 May	<i>Chaenogobius annularis</i>	n.d.	5.280 \pm 0.311 (120)	5.322 \pm 0.430 (20)	0.29
29 May	<i>Leucopsarion petersi</i>		5.710 \pm 0.199 (110)	5.787 \pm 0.312 (20)	2.08
10 July	<i>Tridentiger brevispinis</i>	2.925 \pm 0.153 (121)		3.044 \pm 0.113 (23)	12.63**
10 July	<i>Rhinogobius</i> sp. CB	4.361 \pm 0.168 (151)	4.313 \pm 0.167 (102)	4.404 \pm 0.196 (97)	6.61*

* $p < 0.01$ ** $p < 0.001$ n.d.: no data

peaks before they were caught.

Our findings support the hypothesis that diadromous larval gobioids remain in the tidal river zone for more than a few days, during which time they move upstream and downstream at night and halt in pools or under stones during the day (14), until they acquire the ability to survive in a saline environment.

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